The Life-history of Melicertidium octocostatum (Sars), a Leptomedusan with a theca-less Hydroid Stage.

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With Plate 16.

Contents.

This well-known medusa (fig. 19) is classified among the Thaumantiadae, and is characterized by the presence of eight 'radial' canals on which the gonads are developed. The marginal tentacles are numerous (up to 140) and of unequal size, larger and smaller ones alternating more or less regularly. There are no lithocysts, cordyli or ectodermal ocelli. The manubrium is short, the mouth four-angled and without oral tentacles. The medusa has a fairly wide distribution in the North-east Atlantic ranging from Bergen to Falmouth. (See E. T. Browne, **4**, for details and a discussion of the nomenclature.) The hydroid, as I have ascertained by rearing the eggs, proves to be a hitherto undescribed species identical with one which has been noted for several years (with a year's interval of absence) growing abundantly and spontaneously in the tanks at the Millport Biological Station.

An allied form Melicertum campanula (Agassiz) occurs in West Atlantic Canadian and U.S. waters. In 1863

A. Agassiz (1) described the young hydroid reared from the eggs of *Melicertum*, but this hydroid has not up to the present been recorded in nature from the American coasts.

Development of Eggs of *Melicertidium*.

Ripe examples appeared in the tow-nettings at Millport towards the end of June 1918. By keeping specimens in aquaria in the Research Fellowship Laboratory at Glasgow University I obtained numbers of fertilized eggs. These are small (0·08 mm. in diameter), homogeneous-looking, faintly yellowish in tinge, and with delicate closely-adherent membrane. They are ripe before extrusion and pass outwards through the mouth, as also do the spermatozoa in the males. No membrane of fertilization is formed. Segmentation is total and equal (figs. 1–5), the two-celled stage beginning with a notch or groove on one side of the egg. A blastocoele cavity is recognizable even at the eight- or sixteen-celled stage. Early blastulae are irregular in outline, the blastula wall being a single layer, but exhibiting folds and inpocketings which soon straighten out and do not seem to have any subsequent formative importance (figs. 6 and 7). The larva now becomes pear-shaped, and, having acquired cilia, progresses with the blunt end in front and rotates in the solar direction as viewed from the blunt end (figs. 8 and 9). At this stage the endoderm arises by inward budding from the blastula wall (figs. 8, 9, 10). The budding occurs first near the pointed end, and then all round, gradually filling up the blastocoele cavity, the last part of this cavity to be filled being at the blunt end (fig. 11). The endoderm cells are rounded, slightly granular, and less transparent than the ectoderm. The planula now elongates, becoming almost worm-like, and swims vigorously through the water at any depth. Later it seeks the bottom and becomes attached. The mode of attachment presents certain peculiarities which I hope to elucidate later. The free end becomes swollen and rudiments of the first tentacles appear (fig. 12). Figs. 12–14 illustrate four-tentacled and eight-tentacled stages. Both show a delicate perisarc covering hydrorhiza and hydrocaulus, and ceasing at the base of the hydranth without forming even a rudimentary hydrotheca. At no stage are the bases of the tentacles united by a web or membrane. The sixteen-tentacled stage is entirely similar to young polyps (fig. 15) of the tank hydroid described later in this paper, though the latter are relatively rather larger, no doubt because they could draw during growth on a nutritional reserve greater than was at the disposal of the parent of the colony. This year (1919) I have repeated the rearing experiments and obtained the same results.

Description of the Tank Hydroid.

In the early spring of 1916, 1917, and 1919 colonies of an apparently new theca-less hydroid appeared on stones and on glass in several of the tanks at the Millport Biological Station. Dr. James Ritchie, Royal Scottish Museum, Edinburgh, to whom I sent a specimen in February 1917, made the conjecture, which has proved right, that it might turn out to be the hydroid of some Leptomedusan. A little later in the same year young medusae budded off from a colony were obtained. They had four radial canals, eight tentacles, no lithocysts, and no ectodermal ocelli or oral tentacles. I tried to rear them, but without success. The matter remained there till July 1918, when the results (given above) of rearing Melicertidium eggs unexpectedly connected the tank hydroid with this medusa, and made me undertake more careful experiments (see below) on rearing the young medusae, when these were budded off from the tank colonies in the spring of the present year (1919). The characters of the hydroid are as follows :

Hydranth: entirely theca-less. Tentacles: long, slender, tapering, with solid core of endoderm cells in a single row, studded with nematocysts, not united at their bases by a membrane, arranged in a single circle but tending when fully extended to curve upwards and downwards alternately, commonly sixteen in number, but often more numerous especially in sterile colonies, in which individuals with as many as thirty-two may be noted. Hypostome: conical when closed, shaped like a shallow wide-mouthed urn when fully opened, lined for a very short distance downwards from the margin by close-set columnar cells having the characters of ectoderm. Body of Hydranth: sometimes slender, elongated (1·7 mm. in length), sometimes short (0·9 mm.) or vase-shaped according to contraction, usually showing constriction below hypostome, furnished with stinging cells near middle, merging insensibly into hydrocaulus, except in contracted condition, when junction becomes evident. Hydrocaulus: short but varying in length (1 mm. to 1·7 mm.), often irregularly bent, evidently weak, unbranched except in giving off the stalk of a medusa bud. Hydrorhiza: creeping, branching but not anastomosing, 0·1 mm. across (including perisarc). The distinction between hydrocaulus and hydrorhiza is not always sharply apparent. In the thicker parts of a colony hydrorhizae may intertwine, and leaving the surface of attachment become equivalent to low irregular branching hydrocauli. When, however, the hydrorhizae are not too crowded they remain adherent and give off unbranched hydrocauli. Perisarc: thin, wrinkled irregularly but not ringed, enclosing hydrorhiza and hydrocaulus and separate from these except at occasional points of 'anchorage', thinning away at distal end of hydrocaulus and fusing with ectoderm at base of hydranth which is entirely theca-less. Medusae: Gonophore production takes place from the beginning of February till the end of March. Parts of the colony were isolated, kept in filtered sea-water, and in course of time a number of young medusae were collected. The buds appear at the end of short stems arising from the hydrocaulus well below the base of the hydranth, each hydrocaulus only producing a single medusa. The medusa buds, especially at full size, are more elongated than the free medusae, but the characteristic shape is acquired during the period immediately prior to detachment when vigorous pulsations may be noted. The young medusae have four rather wide radial canals, four tentacles opposite these, four small tentacles or tentacle buds in the interradii, and no lithocysts or ectodermal ocelli (figs. 16, 17, 18). The bell is dome-like and moderately deep: the stomach is quadrangular and the manubrium short, showing four blunt, radially-placed, grooved angles. At first the bell shows a small pit in the middle of the aboral surface, to the bottom of which a cone-like projection of the stomach is anchored. Later this remnant of the connexion between bud and stalk becomes severed, and the summit of the dome shows an upward convexity (fig. 17). Over the rest of the bell, the mesogloea superficial to the plane of the stomach and radial canals forms a relatively thin layer. At their bases the tentacles are hollow and slightly swollen, the endoderm here containing yellowish intracellular pigment. The measurements of the young medusa at rest are: height 1·2 mm., breadth 1·3 mm., interradial diameter of stomach 0·45 mm.; breadth of radial canal 0·06 mm., depth of superficial mesogloea 0·075 mm. The surface of the bell shows numerous minute glancing-points which do not disappear on treatment with acid. The medusae were kept alive for a time, and increased in size; the four interradial tentacles grew almost as big as the radial ones, and new tentacle buds appeared in irregular sequence, one for each interspace between a radial and an interradial tentacle. Stages with ten, twelve, fourteen, and sixteen tentacles were thus obtained. Medusae four weeks old and with *c.* ten tentacles showed a single blunt outgrowth from the stomach in each interradius (fig. 18, *b*). A week later (*c.* twelve tentacles) these outgrowths had extended over the summit of the bell, becoming pointed at their ends. In another week or fortnight (*c.* fourteen to sixteen tentacles) the outgrowths had extended downwards along the sides of the bell and become continuous with slender corresponding upgrowths from the ring canal (fig. 19). I failed to rear the medusae further, but they had already reached the eight-rayed condition characteristic of Melicertidium.

I have not obtained the early four-rayed medusae in townettings off the Millport Station, but they were moderately abundant during April 1919 in plankton from the Gareloch,[1] an inlet farther up the Firth of Clyde.

[1] Since this paper was written, I have found the intermediate stages described above in May plankton from this locality, and the adults at the end of June.

General.

As far back as 1865 A. Agassiz (**1**, p. 130) inferred from the results of tow-nettings that the eight-rayed condition in Melicertum campanula was reached by the formation of four new interradial outgrowths from the stomach in an originally four-rayed young medusa.

Mayer (7, p. 208) thinks that Melicertum campanula (Agassiz) and Melicertidium octocostatum (Sars) are probably identical species, and that Melicertum should have priority as the generic name. However, there are sufficient reasons (especially under (1) and (2) in the following comparison) for keeping Melicertum and Melicertidium as distinct genera, at least in the meantime.

Melicertum (hydroid)	Melicertidium (hydroid)
(1) Tentacles united at their bases by a membrane.	(1) Tentacles not united at their bases by a membrane.
(2) A small theca at base of hydranth.	(2) No theca.
(3) Tentacles up to ten in number.	(3) Tentacles sixteen or more (up to thirty-two) in number.

Melicertum (medusa).	Melicertidium (medusa).
(4) Earliest free stage with only two marginal tentacles.	(4) Earliest free stage with four marginal tentacles and four intervening tentacle buds.
(5) No 'radiating lines' on sub-umbrellar surface.	(5) Numerous 'radiating lines' on sub-umbrellar surface.
(6) Marginal tentacles, in adult equal or sub-equal in size.	(6) Marginal tentacles in the largest specimen examined consist of about sixty small tentacles and about eighty much larger ones.

I agree with Romanes' opinion (**9**, p. 527) that the 'radiating lines' referred to under Melicertidium (medusa) above are bands of muscle fibres, and not of nematocysts as is thought by Browne (**4**, p. 764) and others.

Additional instances in which theca-less hydroids have been reared from Leptomedusae are recorded by Claus (**5**), Metchnikoff (**8**), and Brooks (**2**). The medusae concerned belong to the genus Eutima (McCrady), the species being Eutima campanulata (Claus), Octorchis gegenbauri (Haeckel), in the first two cases, and Eutima mira (McCrady) in the third. Eutima differs from Melicertum and Melicertidium, among other things, in having marginal lithocysts, and in having the stomach mounted on a long peduncle. In the hydroid of E. campanulata, described by Claus and named by him Campanopsis, the tentacles are up to twenty-four in number and are united at their bases by a membrane. A theca is entirely absent, and the young medusae are formed near the middle of the hydranth body. Brooks (**2**) describes the hydroid of E. mira as small, Perigonimus-like, with eight tentacles united at their bases by a membrane.

E. Stechow (**10**) has described a theca-less hydroid, with short hydrocaulus having definitely ringed perisarc, with hydrorhizae forming a network, and with fourteen to eighteen tentacles which were not, so far as could be made out in the preserved material, united at their bases by a membrane. The specimens were in a tube left by a former assistant at Munich and were labelled 'Polyp of Octorchis'. Stechow names it Campanopsis dubia and considers the medusa to have been an Octorchis Eutima.

On the whole, the life-history of Melicertidium supports the generally-accepted view that Leptomedusan hydroids are derived from Anthomedusans. The hydroid is theca-less, the medusa is deep and has no lithocysts or ectodermal ocelli, and though the gonads are on the eight radial canals in the adult, the mode of development of the second four radial canals by outgrowths from the stomach makes it clearly possible that ontogenetically or phylogenetically the gonad tissue of the other four originates in the region of the stomach or manubrium. Indeed, in the earliest stage of the Melicertidium medusa identified by Browne (**4**, p. 763) the gonads extended outwards from the stomach only along the proximal halves of the radial canals.

The Leptomedusan Family Thaumantiadae, to which Melicertum and Melicertidium belong, contains other twelve typical genera. The hydroid stages of only three of these, viz. Thaumantias (Wright, **11**), Laodicea (Metchnikoff, **8**), and Dipleurosoma (Browne, **3**), are known, and, curiously enough, they all possess complete thecae. In having a rudimentary theca Melicertum recalls the Anthomedusan Perigonimus, while Melicertidium having no theca is in line with Eutima (Campanopsis) and Tima, which are members of the Leptomedusan Family Eucopidae. Dr. James Ritchie compares the general facies of the Melicertidium hydranth to that of Halecium. The just liberated medusa of Melicertidium resembles that of Podocoryne carnea except in having a slightly shorter manubrium and no oral tentacles. It is evident that on the borderland between the Antho- and the Leptomedusae there are numerous forms which, whether in their hydroid or their medusoid stages, exhibit features characteristic of better-defined members of either group.

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References.

1. Agassiz, A.—" North American Acalephae ", 'Cat. Mus. Comp. Zool. Harvard ', ii, 1865, p. 130, figs. 202–4.
2. Brooks, W. K.—" On the Life-history of Eutima and on Radial and Bilateral Symmetry in Hydroids ", 'Zool. Anz.', Bd. 7, 1884.
3. Browne, E. T.—" Fauna and Flora of Valencia Harbour ", 'Proc. Roy. Irish Acad.', ser. iii, vol. 5, 1898–1900, p. 696.
4. —— " A Report on the Medusae found in the Firth of Clyde ", 'Proc. Roy. Soc. Edinburgh ', 1905, p. 72.

5. Claus, C.—'Arbeit. Zool. Inst. Wien', Bd. 4, 1881, Heft 1. p. 589.
6. Hartlaub.—'Wiss. Meeres-Untersuch.', Bd. 1, 1894, p. 192.
7. Mayer, A. G.—"Medusae of the World", 'Public. Carnegie Inst. Washington', 109, 1910, vol. i, pp. 207–8.
8. Metchnikoff, E.—'Embryologische Studien an Medusen'. Wien, 1886.
9. Romanes, G. I.—"An Account of some new Species, Varieties, and Monstrous Forms of Medusae", 'Journ. Linn. Soc. Zoology', vol. 12, 1876, pp. 524–31.
10. Stechow, E.—"Ein thecenloser Hydroid der mit einer Leptomedusa in Generationswechsel steht", 'Zool. Anz.', Bd. 41, 1913, pp. 582–6.
11. Wright, T. S.—"On the Reproduction of Thamantias inconspicua", 'Quart. Journ. Micr. Sci.', vol. 2, 1862, pp. 221, 208.

EXPLANATION OF PLATE 16.

Figs. 1–15.—Development of Melicertidium.

Figs. 1–7.—Stages in segmentation and blastula formation of the egg of Melicertidium.

Figs. 8–11.—Change to the planula, formation of endoderm (end), &c. The arrow and circle between 9 and 10 indicate respectively the direction of progression of the larva, and its rotation as viewed from the narrow end.

Figs. 12–13.—Fixation of the larva: formation of first tentacles.

Fig. 14.—Stage with eight tentacles.

Fig. 15.—Portion of a colony, (*a*) hydranth; (*b*) medusa ready for liberation; (*c*) young hydranth and young medusa bud; (*d*) medusa bud almost fully grown; (*e*) hydranth fully stretched out; (*f*) young polypite arising from a hydrorhiza.

Fig. 16.—Just liberated medusa.

Fig. 17.—Aboral part of medusa, two weeks old, showing mesogloeal projection on summit of bell.

Fig. 18, (*a*), (*b*), (*c*).—Stomach and radial canals viewed from above in two days, three weeks, and six weeks' old medusae respectively, showing the formation, by interradial outgrowths from the stomach, of four new 'radial' canals.

Fig. 19.—Medusa, seven weeks old, showing interradial outgrowths from the stomach which have met corresponding upgrowths from the ring canal. R, one of the four original radial canals; I.R., one of the four new interradial canals formed in the manner described above.